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LOCOMOTOR BEHAVIOR DURING PREY-CAPTURE OF A FISHING SPIDER, *DOLOMEDES PLANTARIUS* (ARANEAE: ARANEIDAE): GALLOPING AND STOPPING

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ABSTRACT. Locomotion of *Dolomedes plantarius* Clerck was examined using video analysis. The experiments demonstrate a hitherto unknown aquatic mode of locomotion of *Dolomedes* during prey capture. In a spider running on the water surface the powerful retraction of legs 1, 2 alternates with free flight above the water surface. The stepping cycle in this kind of galloping is five times quicker than in case of ordinary rowing. The experiments also show that the spider may use its elastic safety thread to actively stop its inertial movements after having stopped active locomotion on the water surface. To this end it grasps the thread by the tarsal claw of legs 4. Some ecological aspects of locomotory behavior in *Dolomedes* and the evolutionary origin of aquatic rowing and running are discussed.

Semi-aquatic fishing spiders of the genus *Dolomedes* occupy a heterogeneous habitat of emergent vegetation near open water and localize prey by vibration stimuli of the water surface (Bleckmann 1984; Bleckmann & Barth 1984). After detection of a potential prey the spider moves rapidly over the water surface to capture its prey and then usually returns to its resting place. Its locomotion is a compromise response to the different physical conditions of solid substrates and the water surface (Barnes & Barth 1991). On solid substrates, *Dolomedes* uses an alternating tetrapod stepping pattern as is typical of terrestrial spiders; on the water surface, however, the spider switches to specialized aquatic locomotion with its ipsilateral legs performing a metachronal stepping pattern 4–3–2–1 (Shultz 1987).

Ehlers (1939) briefly describes surface film locomotion in several species of spiders including the initial phase of running towards prey in *D. fimbriatus*: third and then second legs rapidly retract, often followed by retraction of the first legs. Both rowing (Shultz 1987) and wind-assisted movements or "sailing behavior" (Deshefy 1981) of fishing spiders have been studied. Locomotor behavior during prey-capture on the water surface is more complicated than the metachronal stepping pattern during rowing. In this paper two questions regarding the locomotor behavior of fishing spiders are asked: (1) How does the spider move towards its prey? (2) What is the function of the dragline attached to the spider while running on the water surface?

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METHODS

We used subadult males and females of the species *Dolomedes plantarius* Clerck (body length 1.5–2.5 cm) for the experiments. The animals were kept individually in small jars in the laboratory and were not fed for 3–4 days before an experiment. Buzzing flies (*Calliphora vicina*) dropped onto the water surface 5–10 cm away from the spider served as prey stimuli. The spiders formed two experimental groups, (i) intact and (ii) with spinnerets covered by wax.

By using a mirror, the reactions of the spiders to prey were videofilmed simultaneously from above and from the side. For this purpose we used a camcorder (Panasonic NV-MS1E) with "High-Speed-Shutter" positions at $1/500$ s and $1/1000$ s. With a video timer (Panasonic VW-CG2E) reaction times could be determined with a resolution of 0.01 s. Sequences of movements were reconstructed and drawn on the basis of single frame analysis (videorecorder: Panasonic NV-FS 100 HQ, 50 pictures/s). Apart from the movements as such, two additional parameters were determined: distance of passive drifting after having stopped active running towards the fly and speed along the first stretch of the running distance. In each experiment *N* individuals were used to obtain a sample of *n*.

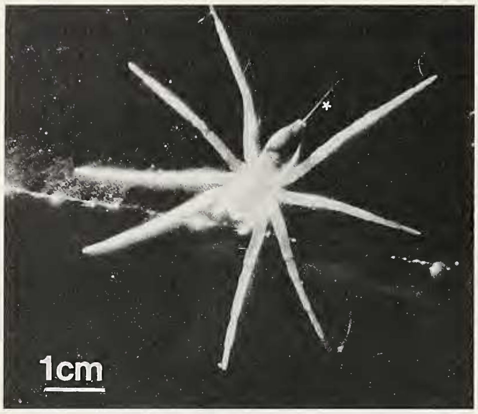

Figure 1.—Resting posture of *Dolomedes plantarius*. Legs L1, R1, and L2 touch the water surface. The spider fastens itself to the solid substrate with a thread, indicated by an (*).

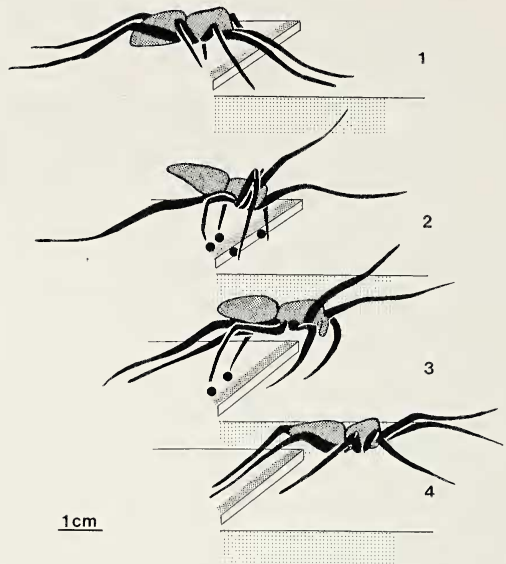

Figure 2.—Jump of hunting spider from the bank towards wave source. Legs 2 and 3 move successively. The sequence 1 to 4 covers a time period of 0.1 s. Black dots show where legs touch solid substrate.

RESULTS

Resting posture.—When resting, *D. plantarius* adopted a posture also typical of other *Dolomedes* species: legs 1 or 1 + 2 or 1 + 2 + 3 contacted the water surface, legs 4 always contacted the solid substrate. When resting the spider fastened itself to some solid substrate with a thread (Fig. 1). If an insect was dropped onto the water surface near the spider, the spider usually responded with prey capture behavior. For intact spiders average reaction time was 1.8 s (SD = ±0.6; $N = 5$; $n = 32$). In spiders with functionless spinnerets the reaction time was significantly longer, measuring 15.8 s (SD = ±6.3; $N = 3$; $n = 10$).

Moving towards potential prey.—When only legs 1 were placed on the water surface, the spider occasionally jumped onto the water by successively moving legs 2 and 3 (Fig. 2). With other leg pairs also contacting the water surface film in its starting position, the spider's reaction consisted of a quick turn followed by running to the wave source. The spider's speed of locomotion in this situation could reach 0.75 m/s (SD = ±0.15; $N = 5$; $n = 45$). During ordinary rowing the speed was only about 0.3 m/s (SD = ±0.08; $N = 5$; $n = 20$). When running towards prey, *D. plantarius* used a leg pattern, which differed from the ordinary rowing leg pattern (Figs. 3, 4): (1) simultaneous abrupt retraction of legs 1, 2 and protraction of legs 3; (2) for a short time the spider had no contact to the water surface; (3) after landing, legs 4 both retracted abruptly (correction of direction); (4) legs 3 retracted. Contralateral legs moved in synchrony. The duration of the stepping cycle was approximately 0.1 s. Spiders with functionless spinnerets and intact spiders did not differ with regard to the movement pattern. As Fig. 3 shows, during such "galloping" the body of *D. plantarius* did not touch the water surface, contrary to its behavior during rowing locomotor mode. While charging, the spider produced a dragline (Fig. 5).

Stopping near prey.—The spider sometimes used its elastic safety thread to actively stop its inertial movements after having stopped active locomotion on the water surface (Fig. 6). To this end it grasped the thread by the tarsal claws of legs 4. The distance of passive inertial movement averaged 1.3 cm for intact spiders (SD = ±0.3; $N = 5$; $n = 18$). For spiders with functionless spinnerets and with no dragline the distance of passive inertial movement increased to 4.5 cm (SD = ±0.5; $N = 3$; $n = 10$).

Course correction after failure.—After having missed a prey animal *D. plantarius* usually rested on the open water waiting for another prey produced vibratory signal. In this situation the reaction time averaged 3.9 s (SD = ±1.2; $N = 5$; $n = 32$) for intact spiders but considerably larger (12.8 s; SD = ±3.0; $N = 3$; $n = 10$) for spiders unable to produce a dragline because of functionless spinnerets. Threadless spiders attracted

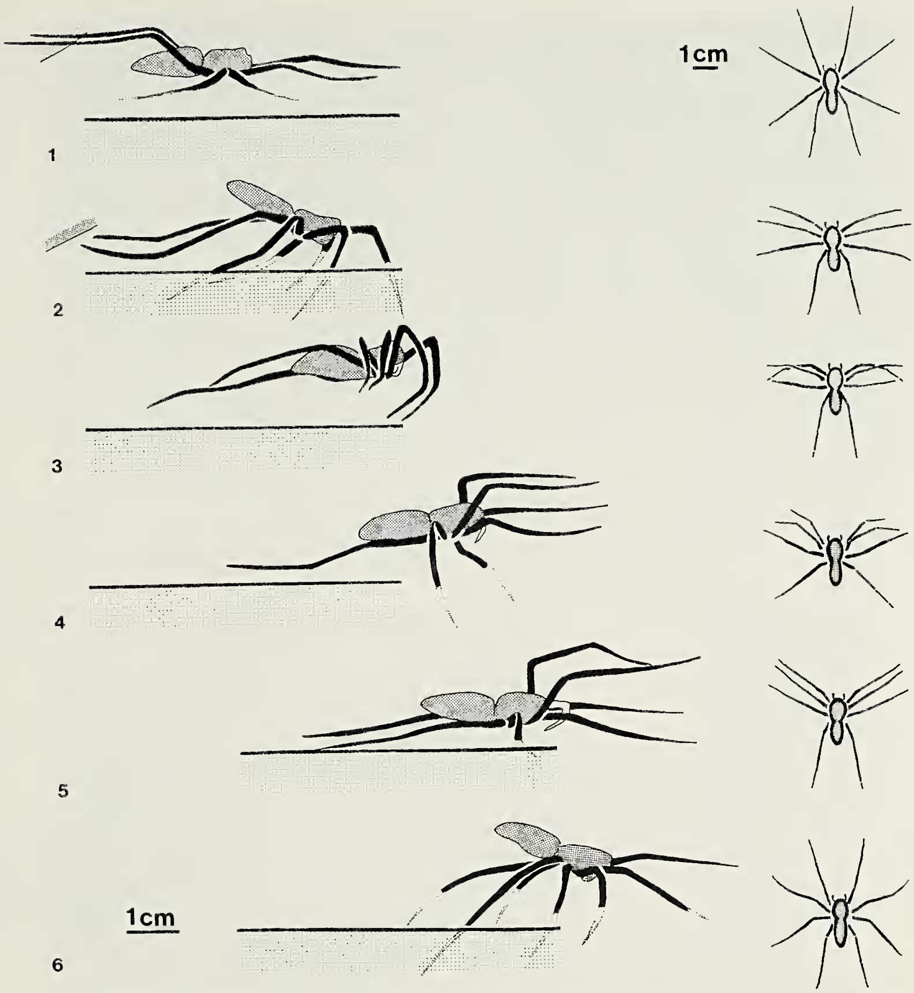

Figure 3.—Kinematics of one stepping cycle during running on the water surface from the side (left) and from above (right). After simultaneous retraction of legs 1 and 2 (2), no leg touches the water (free flight phase) (3). Legs 4 make the directional correction (4, 5). The sequence 1 to 6 covers a time period of 0.1 s.

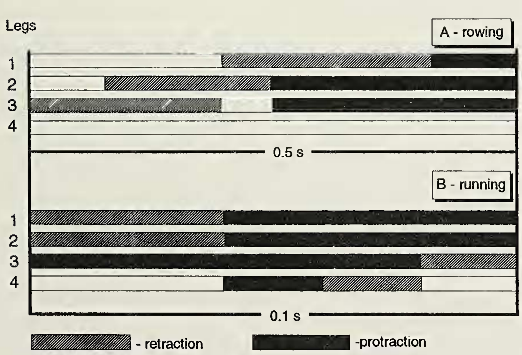

Figure 4.—Gait diagram showing stepping patterns of *Dolomedes triton*, when rowing (after Shultz 1987), and of *D. plantarius*, when running. Contralateral legs move in synchrony.

by potential prey move toward the source of water surface waves at a speed three times greater than that of intact spiders. Intact spiders moved passively around two points: the point of thread fixation by tarsal claw and the point of thread fixation to the solid substrate bordering the body of water from where they started. After having located another prey signal the spider again ran towards the wave source.

Prey capture.—*D. plantarius* caught its prey with its front legs. In case of big prey items, it also used its posterior legs. In this situation all legs were used except the one holding the thread. After having immobilized (caught) its prey, all legs resumed their ordinary resting posture on the water surface. In this situation the spider was

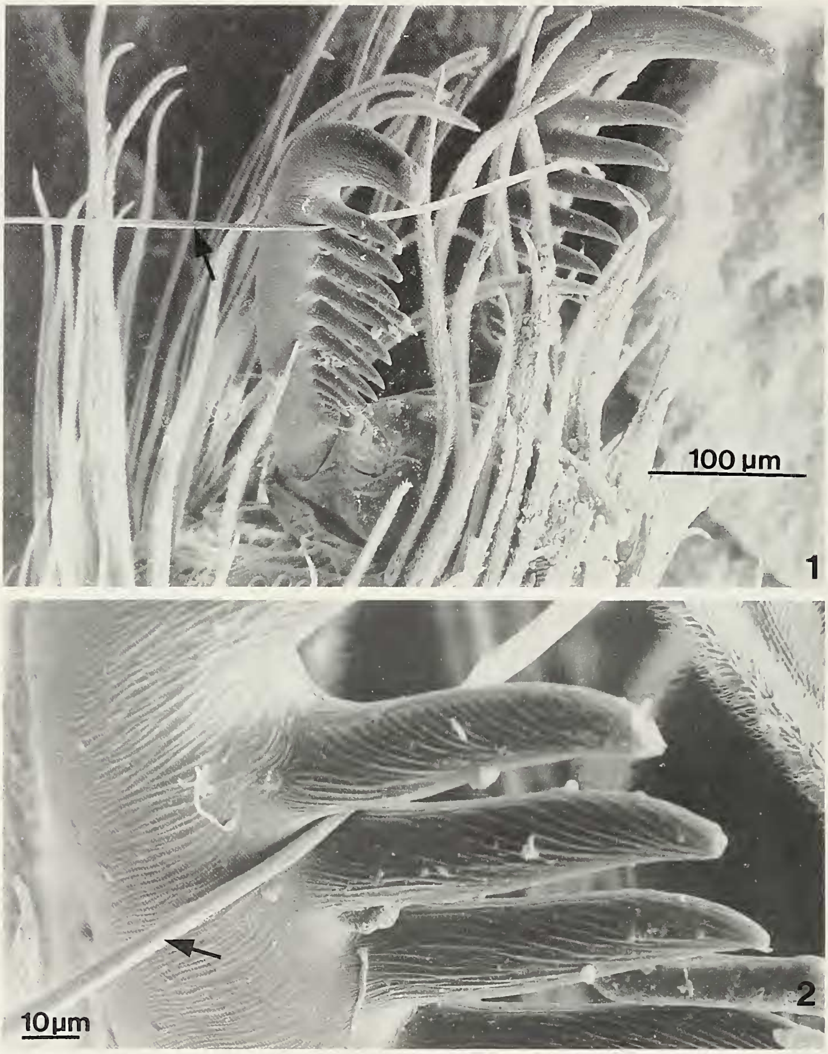

Figure 5.—Scanning electron microphotographs of leg 3 tarsal claws holding a safety thread (arrow).

connected to the solid edge of the water body by its safety thread.

DISCUSSION

Many arthropods have more than one mode of locomotion. Aquatic insects such as beetles (*Dytiscus*, *Hydrophilus*), bugs (families Nepidae, Gerridae, Hydrometridae) (Wendler et al. 1985), anisopteran dragonfly larvae and several species of different spider taxa (Ehlers 1939; Barnes & Barth 1991) both walk on solid substrate as well as row on the water surface.

Locomotion on the water surface.—Schultz (1987) describes ordinary rowing of *Dolomedes triton* quantitatively. He discusses two alternative motor programs adapted for terrestrial or aquatic locomotion. Our experiments demonstrate an additional aquatic motor program for *Dolomedes* (Fig. 4). Thus, two different locomotor patterns exist on the water in different behavioral situations. In a spider running on the water surface the powerful retraction of legs 1, 2 alternates with free flight above the water surface. The stepping cycle in this kind of galloping is five times shorter than in the case of ordinary rowing. This behavior, on the other hand, is similar to rowing in showing synchronized movements of contralateral legs and in correction of direction by legs 4. Running at a speed of more than 0.7 m/s seems to be necessary for *Do-*

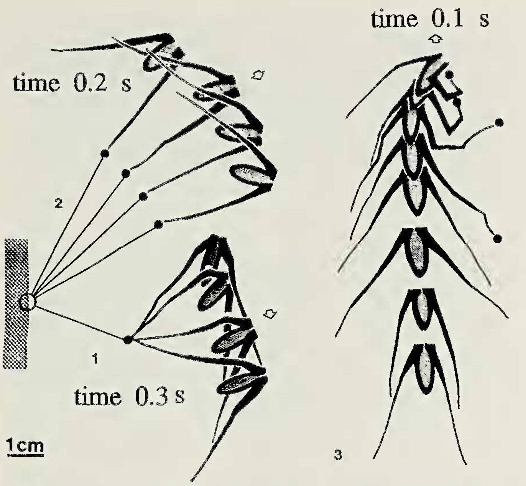

Figure 6.—Kinematics of the movements using a thread: passive movements around the point of thread fixation by tarsus claw (1) and around the point of thread fixation to the solid substrate (2); active stopping by legs 4 movements near the potential prey after running (3). Filled circles show a point of thread fixation by tarsal claws, arrow shows general direction of locomotion. The time periods covered by the phases shown in (1), (2) and (3) are given in the respective figures.

lomedes because its prey may rapidly escape. The synchronous contralateral leg movements and directional correction by legs 4 suggest an identical evolutionary origin of aquatic rowing and running.

Thread.—In several species of different taxa spiders use a dragline (safety thread) to fasten themselves to solid substrate during "normal" locomotion, when dropping and swinging during dispersal behavior (Barth et al. 1991) and when jumping (Parry & Brown 1959) and climbing back (Ehlers 1939). Our experiments show yet another aspect of using such threads. After rapid running spiders need to stop near the prey. Spiders without thread may pass beyond their prey by more than four cm due to inertial forces after having stopped active locomotion. In the natural habitat this distance may be greater, owing to water and wind currents. The thread, which is used for stopping the spider and holding it near the bank, is produced by the spider during running to its prey and during active movements of the posterior legs. Such a thread may also help to support balance during prey capture.

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